how does the visual, tactile, and proprioceptive stimulation generated by self-movement come to specify the self. We do not know when infants develop 'self-recognition' and perceive the synchrony related to their own body movements as belonging to the self. The present studies and those cited above demonstrate that very young infants detect information fundamental to self-recognition. They distinguish between stimulation that is synchronous vs. asynchronous with self-motion and self-touch. Although it is tempting to infer that infants attribute body-related synchrony to the self and are aware that "this is me!", further research will be necessary to explore this intriguing developmental process. Infants likely show a growing awareness of the bodily self, with early differentiation of self from other stimulation and much development thereafter, prior to the age of 15–18 months, when they demonstrate self-recognition according to the well-known rouge test [20].

The Filipetti *et al.* [2] study has added to the growing picture of newborn intersensory capabilities and demonstrates remarkably early sensitivity to body-related visual-tactile synchrony. Together with prior studies of infant sensitivity to proprioceptive-visual synchrony, this raises intriguing questions about the developmental origins of these intersensory skills. Significant prenatal experience is likely involved in developing these skills and the neural architecture to support them and significant postnatal experience is certainly required to refine, develop, and calibrate the senses for developing a richer, more complete sense of the body in space and its relation to other objects and events in the world.

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Evolution: Sex or Survival

A classic paradox in sexual selection is how sexual traits under strong directional selection maintain underlying genetic variation. A new study has found that in Soay sheep a trade-off between reproductive success and survival maintains variation in horn size.

James Howie[1], Andrew Pomiankowski[1,2,*], and Alison J. Cotton[1,2]

Sexual selection provides a compelling evolutionary explanation for the diverse array of sexual ornaments and mating behaviours observed in nature. Yet, at the heart of this theory lies a paradox: male–male competition and female mate preferences cause strong directional selection on sexual characters [1,2]. So, one might expect that allelic variation underlying traits with such important fitness effects would rapidly spread to fixation and denude genetic variation. But empirical evidence shows this is not the case. Traits subject to sexual selection have substantial genetic variation, more so than most ordinary morphological and behavioural traits [2]. A number of plausible hypotheses have been put forward as resolutions of this so-called 'lek paradox', principally relating to genic capture — trait expression depending on multiple genes that underlie an individual's condition [2,3] — and sexually antagonistic selection on alleles that increase the fitness of one sex while decreasing that of the other [4]. However, direct empirical tests remain rare. In a new study, Johnston *et al.* [5] have gone a long way to understanding the major components of genetic variation in horn size, a sexually selected trait in Soay sheep (*Ovis aries*), and turn their findings into a novel solution to the lek paradox.

Soay sheep are a feral population of primitive domestic sheep living on the remote island of Hirta in the St. Kilda archipelago, off the West Coast of Scotland. They have been intensively studied for the last 30 years, with genetic data being collected since 1985

Figure 1. A large horned Soay sheep with big prospects.

RXFP2 genotype affects horn type (normal or scurred). Horny males, such as the one depicted, reproduce better, the rest simply survive. This evolutionary trade-off causes overdominance at the *RXFP2* locus and maintenance of horn size variation in this breed. (Image: Arpat Ozgul.)

[6]. In the rut, males aggressively fight each other in order to monopolize and mate with females as they come into oestrus. The length and thickness of a male's horns (Figure 1) strongly correlates with his mating success [7]. But horn size is highly variable [5]: unlike the majority of males that have normal horns, around 13 percent of the males exhibit vestigial 'scurs', which are unusable in conflicts over females [8]. Females likewise are highly variable. Their horns may be normal (32%), scurred (40%) or non-existent ('polled', 28%) [5].

The persistence of this horn-type variation in males is surprising, as horn size increases a male's reproductive success and detrimental alleles reducing horn size are expected to vanish in the face of selection. The more extensive variation in females is also unexpected. Yet, a recent genome-wide association study, relating ~36,000 single nucleotide polymorphisms (SNPs) to horn phenotype, revealed a surprisingly simple genetic system underlying horn morphology. A single gene, relaxin-like receptor 2 (*RXFP2*) — for which there are two alleles, Ho^{+} and Ho^{P} — explains a large portion of the genetic variation in horn size in both sexes [8]. The Ho^{+} allele is associated with larger horns than the Ho^{P} allele. In males, the Ho^{+} allele is dominant and strongly associated with normal horn morphology, whereas Ho^{P} homozygotes produce normal and scurred phenotypes in equal measure [5]. In females, the three genotypes relate directly to the normal ($Ho^{+}Ho^{+}$), scurred ($Ho^{+}Ho^{P}$) and polled ($Ho^{P}Ho^{P}$) phenotypes. Additional genetic and environmental determinants must exist. But the proportion of phenotypic variation explained by the two known alleles of *RXFP2* is remarkably high [5,8].

To gain a better understanding of selection on the three *RXFP2* genotypes, Johnston *et al.* [5] exploited the long-term information on the Soay population. The task was not small. To obtain reliable estimates of individual reproductive success, Johnston *et al.* [5] constructed a molecular pedigree based on SNPs for 5880 individuals, sampled for blood or tissue between 1980 and 2012. The survival estimates were then obtained from life history data collected annually, allowing a measure of 'overall fitness' to be calculated for each individual in the population and so for their *RXFP2* genotypes (796 males and 954 females).

In males, both $Ho^{+}Ho^{+}$ homozygotes and $Ho^{+}Ho^{P}$ heterozygotes had higher annual reproductive success. But $Ho^{+}Ho^{+}$ homozygotes had considerably lower survival. This made the overall fitness of the heterozygous $Ho^{+}Ho^{P}$ highest. The result is striking. Male $Ho^{+}Ho^{P}$ heterozygotes not only have bigger horns that make them better fighters and able to sire more offspring, but they somehow avoid the trade-off survival cost of this trait. The net effect is overdominance, or heterozygous advantage.

At face value, the results of Johnston *et al.* [5] suggest that an evolutionary trade-off at a single locus operates to maintain genetic and phenotypic variation in a secondary sexual trait. This augments a limited list of cases supporting heterozygote advantage [9,10]. The result suggests that the standard explanation of sexual trait variation does not stack up. The genic capture hypothesis proposes that many genes of small effect should contribute to variation [2,3], whereas in this case, the *RXFP2* locus explains most of the genetic variation in horn size [5,8]. In addition, sexual antagonism seems to play little role, as there was no effect of *RXFP2* genotype on female reproductive success, survival, or overall fitness.

However, reality is likely to be more complex, and the extent to which wider conclusions can be drawn is unclear. The presence of overdominance is itself paradoxical. As the Ho^{P} allele occurs at a frequency of ~0.5 in the population, around one half of the male population exhibit suboptimal fitness, either lacking horns and failing in reproduction, or suffering considerable survival loss associated with the horned phenotype. Another way of thinking about this is to ask why $Ho^{+}Ho^{P}$ heterozygotes have high survival even though they have large horns. One possibility is that males with the $Ho^{+}Ho^{P}$ produce slightly smaller and thinner horns [8]. This locus also affects time to sexual maturity [11], suggesting that $Ho^{+}Ho^{+}$ homozygotes overshoot the timing or size of optimum horn growth, gaining little or no further reproductive success, but incurring a loss in viability. But this then begs the question why no modifier genes have arisen that would limit horn growth in $Ho^{+}Ho^{+}$ homozygotes.

Another complication lies in the origins of Ho^{P}. This allele is thought to have been favoured under early domestication as it is associated with distinct scurred or polled phenotypes among many domestic breeds [5,11]. What is less clear is whether the current

St. Kilda Ho^P alleles are those that have been present since the island was first colonized or reflect subsequent, perhaps recent, admixture of sheep form elsewhere. For instance, coat colour polymorphisms in Soay sheep reflect admixture with modern breeds in the last 150 years [5]. So the Soay population might have been introgressed by superior Ho^P alleles that conceivably confer positive fitness effects through pleiotropy or close linkage with other genes. This view gains some support as over the last 20 years the Ho^P allele has been increasing in frequency in the population by ~20%. However, this rate of increase need not be the result of selection as it is not distinguishable from random fluctuations through drift [5].

The lesson from this study is simple. Pin-pointing the genetic basis of sexual traits in natural populations is likely to throw up challenging observations. It's too early to conclude that overdominance at single loci will play a large role in explaining the lek paradox, or that genic capture and sexual antagonism play no part. But, the vast diversity of bizarre and extravagant ornamentation and weaponry used in courtship is ripe for an unraveling of its genetic basis.

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Colour Vision: Parallel Pathways Intersect in *Drosophila*

In the last one hundred years, colour vision has been demonstrated in bees and many other insects. But the underlying neural wiring remained elusive. A new study on *Drosophila melanogaster* combining behavioural and genetic tools yields surprising insights.

Almut Kelber and Miriam J. Henze

Ninety-nine years after Nobel prize winner Karl von Frisch proved that honeybees see flowers in colour [1], bees are among the best-studied animals with respect to colour vision. Their eyes house photoreceptors sensitive to ultraviolet (UV), blue and green light. The signals from these three receptor types are compared neurally for very fine colour discrimination, limited only by receptor noise [2,3]. However, studies of the neural substrate of colour vision beyond the photoreceptor level have proven frustrating. Honeybee neurons were difficult to penetrate, signals were hard to interpret, and genetic tools are still unavailable. At this point, the fruit fly *Drosophila melanogaster* enters the colour vision scene. Flies, including *Drosophila*, have long been models for visual transduction and motion vision [4], but colour vision research rarely considered *Drosophila* a useful model species: fruit flies were thought to have an extremely derived colour vision system, and on top of that, they don't seem to care much about colour. Behavioural tests using phototaxis or aversive conditioning by electric shocks or heat [5,6] did not allow for studies of fine colour discrimination. Recently, however, the group of Hiromu Tanimoto and colleagues developed a method to train fruit flies to associate a light stimulus with a sugar reward [7]. In a new study [8], in this issue of *Current Biology*, they now combine the new behavioural method with genetic tools to unravel novel and important secrets of insect colour vision.

First, Schnaitmann, Tanimoto and colleagues [8] demonstrated that fruit flies learn to discriminate blue and green. In the critical test, they trained fruit flies with dark blue and light green and showed that the flies chose the correct colour even when intensities were inversed. Second, and more importantly, the authors asked which photoreceptor cells their flies used for this colour discrimination — with an astonishing result. To understand the importance of their finding, we have to take a closer look at the eyes of bees and flies and colour vision in general.

Colour vision — the ability to discriminate colour stimuli independent of intensity — requires at least two types of receptor with different, preferably narrow, spectral sensitivities. Signals from these receptors need to be compared in the colour vision pathway. By contrast, pattern, shape and motion vision rely on broadly tuned achromatic signals that do not include colour information. In humans, red and green cones contribute to both, the achromatic and the colour vision pathway. For achromatic vision, signals from red and green cones are summed in retinal ganglion cells. For colour vision, signals from red cones excite